Why help? Relationship quality, not strategic grooming predicts infant-care in group-living marmosets

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Title: **Why help? Relationship quality, not strategic grooming predicts infant-care in group-living marmosets**

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Abstract

Cooperatively breeding common marmosets raise their infants with the help of other adult group members, but individual care-taking contribution can vary considerably. We tested four hypotheses that may explain this variation within marmoset family groups. The pay-for-help hypothesis argues that allogrooming is used strategically by parents to pay helpers for helping. The pay-for-infant-access hypothesis claims that helpers use allogrooming as payment for infant-access. The intrinsic predisposition hypothesis suggests that more affiliative individuals are also more motivated for infant-care, and the relationship quality hypothesis that individuals involved in highly affiliative relationships with main caregivers contribute more to infant-care. To test these hypotheses, we followed five marmoset family groups over a total of eight reproductive cycles, and quantified affiliative behavior, infant-carrying, and food sharing over six to 12 weeks around infant-birth. We found no evidence for either the pay-for-help or pay-for-infant-access hypotheses nor did intrinsic prosocial predisposition determine individual infant-care. Mutual dyadic affiliation, however, was positively linked to infant-carrying and food sharing in female and male breeders and in male helpers. This suggests that cooperation during infant-care is mediated by relationship quality rather than strategic grooming in marmosets. Overall, these results may also contribute to a better understanding of cooperation in humans.

Key words: common marmoset, infant-care, prosociality, relationship quality, pay-for-infant-access, pay-for-help

1. Introduction

Common marmosets live in small family groups that consist of a dominant breeding pair and non-reproductive helpers, and in which all group members participate in rearing dependent offspring [1, 2]. Allomaternal care provided by male breeders and helpers of both sexes can ultimately be understood in terms of direct and inclusive fitness benefits [3-5]. Nevertheless, individuals show considerable variation in allomaternal care, which cannot be explained by variation in relatedness [6-8]. One possible explanation for this variation is that individuals strategically use affiliative behaviors toward others to manipulate their care-giving contributions, e.g. by paying others for helping. An intriguing alternative explanation is that high quality relationships among marmoset care-takers are characterized by increased levels of non-strategic affiliation, and that relationship quality is associated with individual infant-care contribution.

Strategic affiliative interactions may be used to enforce individual interests, such as gaining coalitionary support in fights, or access to other commodities such as tolerance, mating opportunities, and young infants [9-11]. For instance, grooming can promote the formation of coalitions and agonistic support in males and females [12, 13] (e.g. in chimpanzees [14] and Japanese macaques [15]). Grooming can furthermore increase tolerance over food (e.g. in tufted capuchin monkeys [16] and Japanese macaques [15]), reduce tension (e.g. in long-tailed macaques [17]), and be used in conflict resolution (e.g. in chimpanzees [18] and reviewed in [19]). In species with allomaternal care, grooming and affiliation may also be used by breeding individuals as incentive or reward for potential helpers to engage in care-taking [20, 21] or by subordinate helpers to buy access to young infants [22, 23].

Repeated affiliative interactions, especially allogrooming [24, 25], are also a key element in the formation and maintenance of social relationships in primates. Dyadic affiliative interactions and grooming are meaningful estimators of the quality and value of relationships [26], as evident in many primates [27-30]. In marmosets, strongly bonded partners evidently groom each other more and show synchronized baseline levels of oxytocin

72 [31] – a neurohormone that regulates bonding and affiliation in mammals [32]. Strong and
73 stable relationships are ubiquitous in marmoset breeding pairs, which are usually described as
74 socially monogamous [33]. Such relationships also occur in dyads other than the breeding pair
75 (i.e. in breeder-helper dyads and in helper-helper dyads), and remain stable up to six months
76 [31, 34]. There is increasing evidence that, in many primate species, strong social bonds
77 involve cooperative interactions that are functionally adaptive [35-38]. However, so far, this
78 question has not been addressed explicitly in marmoset monkeys, neither for breeding pairs
79 nor for other dyads. We hypothesize that one potential function of strong relationships in
80 marmoset family groups may be a facilitating effects on individual cooperativeness.
81 Affiliation between adults may thus be related to individual care-taking contributions
82 in marmosets in strategic or non-strategic ways: Strategic usage of affiliation underlies (i) the
83 pay-for-help hypothesis and (ii) the pay-for-infant-access hypothesis, whereas non-strategic
84 usage of affiliative interactions suggests (iii) the intrinsic predisposition hypothesis and (iv)
85 the relationship quality hypothesis. These hypotheses predict different sets of grooming
86 patterns within families and differential links between directed grooming or dyadic affiliation
87 and individual contributions to infant-care, as summarized in Table 1.
88
89 ***Strategic affiliation***
90 First, directed grooming may be used strategically by parents to "pay" other group
91 members for help during infant-care (pay-for-help hypothesis). In contrast to most other
92 primates [39], grooming asymmetries in marmosets are typically reversed and dominant
93 parents groom subordinate helpers more rather than vice versa [21, 40]. This has led to the
94 hypothesis that female breeders groom male breeders more and parents groom subordinate
95 helpers more as incentive to stay and help rearing offspring [20, 21]. This hypothesis is
96 supported by the finding that during pregnancy, wild tamarin female breeders spent more time
97 grooming male breeders compared to postpartum or non-reproductive periods. However,

female breeders also received more grooming from male breeders during this time [20]. Furthermore, Ginther and Snowdon [41] found increased grooming levels from pregnant tamarin females towards adult male helpers who had been most engaged in care-taking in the previous litter. Together, this suggests that female breeders may actively strengthen the bonds with their mates and male helpers, especially prior to birth, e.g. to keep them committed to help. Lazaro-Perea et al. [21] investigated grooming from female breeders to female helpers as reward for asymmetric services in wild groups of common marmosets. They found group-size dependent grooming of female breeders to female helpers, but no relation between grooming received by female helpers and participation in territorial defense. Crucially, to our knowledge it has never been directly investigated if directed grooming received from female or male breeders is indeed linked to subsequent helping in callitrichid helpers. To evaluate the pay-for-help hypothesis, we therefore tested the predictions that more grooming (before and after the birth of dependent offspring) is directed from female to male breeders, and from parents to helpers than vice versa, and that *grooming received* from female breeders and male breeders is positively linked to care-taking behavior in male breeders and helpers, respectively.

Second, subordinates, in particular female helpers, may use grooming to buy access to infants and maybe tolerance during care-taking from dominants (pay-for-infant-access hypothesis) [22, 23]. This strategy has been reported in independently breeding female long-tailed macaques [23], baboons [42, 43], golden snub-nosed monkeys [44], patas monkeys [45], vervet monkeys [46], and capuchins [47]. Payment for infant-access is typically expected in species where mothers do not rely on allomaternal care and are reluctant to share their babies [22, 48], but it is not expected in cooperatively breeding species, where allomaternal care benefits infants and female breeders [49]. However, in cooperatively breeding marmosets, contributing to infant-care is not always equally possible for all potential care-takers, because infants can only be carried by one individual at the same time, and care-

takers also compete over infant-access [50-52]. In particular female helpers are not always permitted by other group members to handle and carry infants, despite being strongly motivated to do so [53], or they are allowed to carry them only after several weeks postpartum [6]. This can most likely be explained by divergent reproductive tactics of male and female marmoset helpers: Reproductive competition is much higher for females than for males in marmosets, since breeding is usually limited to only one female per group which is dependent on the other group members´ help in rearing her offspring [54]. Hence, under some conditions, female helpers may pose an infanticidal threat due to high reproductive competition among females [8, 55, 56]. The pay-for-infant-access hypothesis thus predicts that helpers, especially females, groom their parents more than vice versa, and that *grooming given* from helpers to parents is positively linked to infant-carrying of helpers. We did, however, not expect such a link between *grooming given* from helpers to parents and the helpers´ food sharing with infants, because food sharing can be performed ad libitum by all individuals [6].

Non-strategic affiliation

Third, in contrast to the first two strategic hypotheses (pay-for-help and pay-for-infant-access), the intrinsic predisposition hypothesis predicts that higher intrinsic prosocial motivation drives some individuals to groom their group members more and to also engage more in infant-care. This hypothesis thus predicts a positive correlation between *grooming given to all* other group members and infant-care contribution.

Finally, individual cooperativeness may be positively linked to the quality of the individuals' dyadic relationships with specific partners (relationship quality hypothesis). This is consistent with the results reviewed by Seyfarth and Cheney [35], which show that strong social bonds or friendships often involve cooperative interactions and are adaptive in many mammal species. For instance, bond strength and relationship quality among males have been

shown to predict future cooperation in agonistic coalitions and thus enhanced social dominance and paternity success (e.g. in Barbary and Assamese macaques [57, 58], reviewed by Ostner and Schülke [59], van Hooff and van Schaik [60]) and they improve the coordination and efficiency of cooperative defense against predators (e.g. in crested macaques [61]). Furthermore, in chimpanzees, bonding facilitates the sharing of information via food-associated calls [62] and cooperation during hunting [63], food sharing [64], and territory defence [65]. Overall, social bonding is associated with fitness benefits in humans and non-human primates, including decreased mortality risk and increased life span [38, 66], and increased reproductive success (infant survival, shorter birth intervals) [37, 67-70]. In cooperatively breeding primates, joint infant-care may therefore be facilitated by strong social bonds, in particular between breeders but also in breeder-helper dyads. The relatively higher mutual grooming levels in breeders of cooperatively breeding tamarin monkeys during pregnancy [20] may in fact well reflect mutual investment to enhance cooperation during care-taking after infant-birth. However, positive consequences of high dyadic relationship quality on cooperativeness during infant-care in group-living callitrichids, such as marmosets and tamarins, have not been investigated so far. To test the relationship quality hypothesis in marmosets, we therefore predicted that higher relationship quality (higher average levels of *mutual dyadic affiliation)* is positively linked to individual infant-care contribution after birth. This is particularly expected in dyads who engage extensively in infant-care like breeding pairs and breeder-male helper dyads.

Hypothesis		**Dyad type**	**Expected type of affiliative interaction**	**Expected link to care-taking**	**When?**
Strategic effects	***pay for help***	breeder-breeder	directed grooming: females → males	**in males:** positive correlation with ***grooming received from females***	pre-birth and post-birth
		breeder-helper	directed grooming: breeder → helper	**in helpers:** positive correlation with ***grooming received from breeders***	
	pay for infant-access	breeder-(female) helper	directed grooming: (female) helper → breeder	**in (female) helpers:** positive correlation with ***grooming given to breeders*** (only carrying)	

Non-strategic effects	***intrinsic predisposition***	all dyads	directed grooming: individual → all others	**in all individuals:** positive correlation with mean ***grooming given to others***	pre-birth
	relationship quality	breeder-breeder breeder-(male) helper	mutual dyadic affiliation	**in both partners:** positive correlation with ***mutual affiliation***	

Table 1: Predictions of the four hypotheses with regard to expected links between affiliative interactions and infant-care behavior in group-living marmosets.

To test the predictions of these four hypotheses (Table 1), we studied five family groups of captive marmosets over a total of eight reproductive events. We recorded directed grooming and mutual dyadic affiliation before and after birth. Individual cooperativeness was estimated based on infant-carrying and food sharing after infant-birth.

Potential effects of strategic grooming as payment for help or for infant-access were assessed separately for the pre- and post-birth period, to be able to capture both long- and short-term effects. Since pre-birth grooming precedes the actual helping situation, it might be related to long-term relationship management rather than functioning as direct strategic payment. In contrast, post-birth grooming is more likely to be associated with more immediate effects, including tension reduction or tactical behavior. To assess the link between intrinsic prosocial predisposition or relationship quality with individual care-taking contribution, we only used data from the pre-birth period. We chose to do so because post-birth affiliation often occurs in the presence of infants and may thus rather reflect behavioral interactions that are directly related to infant-handling, care-taking, or strategic behavior (hypothesis (i) and (ii) in Table 1).

2. Methods

2.1. Study animals

We observed five marmoset groups (26 individuals) during eight reproductive events over six to 12 weeks, starting three to one weeks prior to birth. In two reproductive events, observations only started with infant-birth, hence pre-partum analyses are based on six reproductive events. Reproductive event order, group identity, sampling protocols, and individual sex and status of all studied individuals are listed in supplementary Table S1. Ten individuals from two groups were sampled repeatedly during different reproductive events, but only five individuals from one group (Lancia) also occurred repeatedly in the analysis of pre-birth behavioral effects, since for the other group (Nina) no pre-birth behavioral data were available in the second and third reproductive event.

All groups were housed in standardized enclosures (depending on group size, one or multiple basic cage units; each measuring 2.4 m height x 1.5 m depth x 0.8 m width). All enclosures were connected to spacious outdoor areas and equipped with a sleeping box, a water dispenser, several wooden climbing structures, an infrared lamp and a mulch floor. The animals were housed under natural light with additional artificial light on a 12 h/12 h light–dark cycle and UV light (300W). Their diet consisted of a vitamin and calcium-enriched porridge in the morning, fresh fruits and vegetables over midday, and gum and mealworms in the afternoon. Water was available ad libitum.

2.2. Behavioral observations

During each reproductive event, we observed affiliative interactions (grooming and huddling) among adult marmoset group members. Agonistic interactions were rare and therefore not analyzed in the present study. Grooming (picking the fur or skin of another individual with hands or mouth) and huddling (resting in direct body contact with another

218 individual) were recorded based on either group scans (reproductive events 1-4) or continuous
219 observations (reproductive events 5-8). Group scans were performed three times per week for
220 each group, recording all affiliative interactions between all adult group members over two
221 hours every five minutes (24 scans per observation day and group). Continuous observations
222 were performed three times per week for each group (between 9–12 am or 1–5 pm) as group
223 focal observations of 50-60 minutes per group (10 minutes for each group member), in which
224 specific dyadic affiliative interactions among all group members were recorded. To assess the
225 link between dyadic relationship quality and individual care-taking, we estimated mutual
226 dyadic affiliation as an indicator of relationship quality for each dyad. To do so, we combined
227 total within-dyad grooming (the sum of "individual A grooming B" and "individual B
228 grooming A") and huddling (of individual A and B) into one mutual affiliation value per
229 dyad, by summing up the durations (or number of scans) of each behavioral measure. Average
230 values of directed grooming and mutual dyadic affiliation were then calculated for the pre-
231 birth and post-birth observation periods as percent of total scans (100*scans grooming
232 given/total scans) or of total time observed (100*seconds grooming given/total seconds
233 observed), respectively. Importantly, all average values were z-transformed prior to analyses
234 in order to eliminate potential variation in absolute values resulting from the different
235 recording methods in reproductive events 1-4 and 5-8.

236 For each individual, infant-carrying was recorded daily between 8 am and 5 pm in
237 hourly group scans over 100 days after birth. Food sharing was assessed experimentally as
238 described in Finkenwirth et al. [6] and Martins et al. [71]. During the postpartum study period,
239 we tested each individual two to three times per week (between 9–12 am or 1–5 pm), by
240 presenting five food items one after another to the focal adult individual, and recording the
241 frequencies and characteristics of sharing with infants (direction, vocalizations, begging
242 intensity, pro- and reactivity). We used both reactive (after infant begging) and proactive
243 sharing (initiated by the food possessor without infant begging) to estimate individual food

sharing levels. Carrying was expressed as percentage of the total number of scans (100*scans carried/total scans) and food sharing as percentage of shared food items relative to the total number of food items received (100*shared food items/total food items received).

2.3. Statistical analyses

We investigated the link between dyadic affiliative behaviors (directed grooming and mutual dyadic affiliation) and individual infant-care contribution (infant-carrying and food sharing) in reproductive marmoset groups.

First, in part a), we conducted a set of linear mixed models to analyze the overall link between dyad type and directed grooming (separately for pre-birth grooming and post-birth grooming), as well as the link between directed grooming and infant-care behaviors. To do so, we coded each combination of dyad type resulting from the different classes of animals (i.e. male breeder, female breeder, male helper, female helper) in both directions. Individuals nested in dyad, dyads nested in group, and reproductive event nested in group were included as random effects. For the analysis of grooming patterns, we included dyad type as fixed factor in the full models. For the analysis of infant-care behaviors, we included dyad type, directed grooming, and the interaction between the two as fixed factors. We then determined whether the full models explained variation in directed grooming and infant-care behaviors better compared to the null models that only contained random effects, based on the Akaike information criterion (AIC). If this was the case, we used post-hoc tests (parts b – e) to test the specific predictions resulting from the hypotheses summarized in Table 1. As post-hoc tests we used Wilcoxon Signed Ranks tests and permutation Spearman correlations that included a bootstrapping step to control for dyadic dependencies in the data and for the repeated occurrence of individuals that were sampled twice in different reproductive events.

In part b), we tested whether directed grooming was used strategically as payment for help from female to male breeders and from breeders to helpers (pay-for-help hypothesis). To do so, we tested whether grooming (without infants) in the pre- and post-birth period was more directed from female to male breeders than vice versa, and from breeders to helpers than vice versa, using Wilcoxon Signed Ranks Test. In the post-birth period, we tested whether grooming received from male breeders by female breeders and from helpers by breeders was positively linked to infant-carrying or food sharing in male breeders and male and female helpers (grooming recipients), respectively. To do so, we performed permutation Spearman correlations.

In part c), we investigated whether directed grooming was used strategically as payment for infant-access from helpers to breeders (pay-for-infant-access hypothesis). We tested whether grooming in the pre- and post-birth period was more directed from helpers to breeders than vice versa, using Wilcoxon Signed Ranks Test. Furthermore, we tested whether grooming given from helpers (especially females) to breeders was positively linked to infant-carrying in helpers (grooming donors), again using permutation Spearman correlation.

In part d), we investigated whether more affiliative individuals were also more cooperative, i.e. whether non-strategic grooming was linked to more care-taking of the groomer (intrinsic predisposition hypothesis). To do so, we tested the link between individual mean levels of grooming given to all other group members before birth with the groomers' infant-carrying and food sharing levels, using linear mixed-effect modelling with restricted maximum likelihood estimation (R version 3.1.3, lme package). Infant-carrying or food sharing were used as dependent variable, sex and status were used as fixed factors, and individual nested in group was used as random factor. The best-fitting model was selected based on the Akaike information criterion (AIC) estimation. Approximate normality and homogeneity of model residuals was assessed by visual inspection of residuals plotted against fitted values and a qq-plot. All model assumptions were met.

In part e), we tested whether pre-birth dyadic relationship quality was positively linked to care-taking of breeders in breeding pairs or of breeders and helpers in breeder-helper dyads (dyadic relationship quality hypothesis). To do so, we first correlated pre-birth dyadic mutual affiliation values from breeding pairs with individual food sharing and infant-carrying rates of breeders, and dyadic affiliation values from female breeder-helper and male breeder-helper dyads with food sharing and infant-carrying rates of female and male breeders, and helpers, using permutation Spearman correlations.

3. Results

a) General results

In the first GLMMs, we found that variation in grooming was better explained in a model that included dyad-types compared to a null model that only included random effects, both for pre-birth grooming (ΔAIC = 98.13) and post-birth grooming (ΔAIC = 13.8). The full models for infant-care behaviors (food sharing and carrying) included dyad types, directed grooming (pre- or post-birth), and the interaction between dyad type and directed grooming. All full models fit the data better compared to the null models (food sharing/pre-birth grooming: ΔAIC = 631.34, food sharing/post-birth grooming: ΔAIC = 902.17, infant carrying/pre-birth grooming: ΔAIC = 573.29, infant carrying/post-birth grooming ΔAIC = 858.57). We therefore continued to test the specific predictions of our hypotheses with post-hoc tests, as detailed below.

Strategic affiliation

b) Pay-for-help hypothesis

320

321 ***Breeder-breeder dyads – do females pay males for help?***

322 In contrast to the prediction, female breeders did not groom male breeders more than
323 vice versa, neither before birth (Z=-1.78, p=0.075, N=6) nor after birth (Z=-1.26, p=0.208,
324 N=6). Consistent with the pay-for-help hypothesis, pre-birth grooming by female breeders to
325 male breeders was indeed positively linked to infant-carrying by male breeders (Rho=0.83,
326 p=0.042, N=6, Figure 1A). However, a similar effect was also found for the opposite
327 direction, i.e. pre-birth grooming by male breeders was positively linked to infant-carrying by
328 female breeders (Rho=0.89, p=0.019, N=6, Figure 1A). Hence, both male and female breeders
329 are more engaged in infant-carrying when they receive more grooming from their mate before
330 birth. This rather supports the relationship quality hypothesis (see below). Furthermore, pre-
331 birth grooming from female breeders to male breeders was positively linked to food sharing in
332 male breeders (Rho=0.83, p=0.042, N=6, Figure 1B), whereas male breeders grooming
333 female breeders was not associated with female breeders' food sharing (Rho=0.54, p=0.266,
334 N=6). No link was found between post-birth grooming from female to male breeders (and
335 vice versa) and either infant-carrying (male breeders: Rho=0.10, p=0.823, N=8; female
336 breeders: Rho=-0.12, p=0.779, N=8) or food sharing (male breeders: Rho=0.52, p=0.183.
337 N=8; female breeders: Rho=-0.33, p=0.420, N=8) of the grooming recipients.

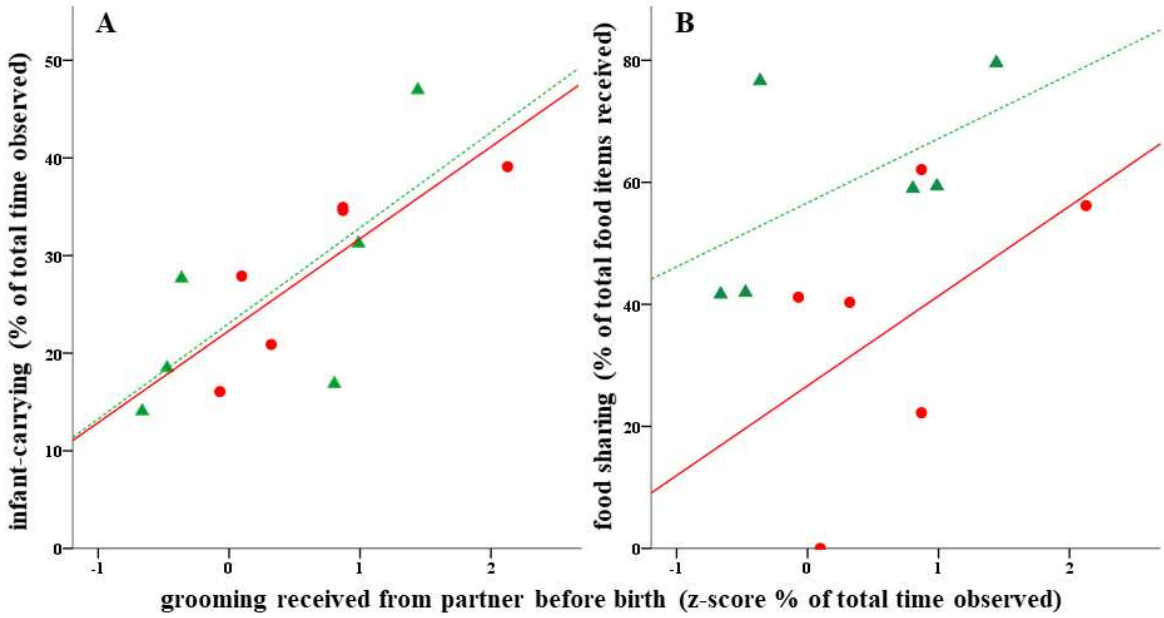

Figure 1: Positive link between grooming received and infant-care behavior. Grooming (z-score % of total time observed) received from the partner prior to birth in marmoset breeders is positively linked to infant-carrying (A, % of total time observed) in male breeders (green triangles, dotted lines) and females (red circles, solid lines) , and to food sharing (B, % of total food items received) in males but not females .

Breeder-helper dyads – Do breeders pay helpers for help?

Grooming directions and the link between directed grooming and care-taking in helpers were analyzed separately for female breeder-female helper, female breeder-male helper, male breeder-female helper, and male breeder-male helper dyads. Female breeders did not groom female helpers and male helpers more than vice versa (female helpers: pre-birth: Z=-0.09, p=0.929, N=11; post-birth: Z=-0.72, p=0.469, N=16; male helpers: pre-birth: Z=-1.01, p=0.314, N=9; post-birth: Z=-1.41, p=0.158, N=14). Male breeders also groomed neither female helpers nor male helpers more (female helpers: pre-birth: Z=-1.60, p=0.109, N=11; post-birth: Z=-0.827, p=0.408, N=16; male helpers: pre-birth: Z=-1.25, p=0.213, N=9; post-birth: Z=-1.73, p=0.084, N=14). However grooming towards all helpers combined was

355 significantly higher from male breeders to helpers than vice versa before birth (Z=-2.09,
356 p=0.036, N=20).
357 The grooming patterns thus partially correspond to the predictions of the pay-for-help
358 hypothesis. However, we found no evidence that grooming from breeders increased infant-
359 care contribution of helpers, since neither pre-birth nor post-birth directed grooming from
360 breeders to helpers was positively linked to helpers' infant-carrying or food sharing
361 (supplementary Table S2). Rather, there was a negative link between pre-birth grooming by
362 male breeders and post-birth food sharing in helpers (Rho=-0.51, p=0.031, N=18). This effect
363 specifically occurs in female helpers (Rho=-0.69, p=0.026, N=10), whereas it is absent in
364 male helpers (Rho=0.16, p=0.713, N=8).
365
366 **c) Pay-for-infant-access hypothesis**
367
368 ***Breeder-helper dyads - Do helpers pay breeders for access to infants?***
369 Helpers did not groom their parents more than vice versa before birth (see results part
370 b). Furthermore, neither pre- nor post-birth grooming from helpers to parents was linked to
371 infant-carrying in helpers after birth (female helpers grooming female breeders: pre-birth:
372 Rho=-0.41, p=0.235, N=10; post-birth: Rho=-0.08, p=0.794, N=14; female helpers grooming
373 male breeders: pre-birth: Rho=-0.25, p=0.483, N=10, post-birth: Rho=0.09, p=0.742, N=14;
374 male helpers grooming female breeders: pre-birth: Rho=0.14, p=0.736, N=8; post-birth:
375 Rho=0.02, p=0.957, N=12; male helpers grooming male breeders: pre-birth: Rho=0.14,
376 p=0.736, N=8; post-birth: Rho=0.48, p=0.114, N=12).
377
378 ***Non-strategic affiliation***
379
380 **d) Intrinsic predisposition hypothesis**

We found no indication that more affiliative individuals also contributed more to infant-care in their groups, since individual mean levels of grooming given to all other group members before birth were neither positively linked to infant-carrying (Linear model estimate=1.97, t=1.13, p=0.320) nor to food-sharing (Linear model estimate=0.03, t=1.48, p=0.214; supplementary Table S3).

e) **Mutual dyadic relationship quality hypothesis**

Breeder-breeder dyads

When testing the link between dyadic relationship quality (based on mutual dyadic affiliation) and individual care-taking contribution in breeders, we found that pre-birth dyadic affiliation was positively related to infant-carrying in both female breeders (Rho=0.89, p=0.019, N=6) and males (Rho=0.83, p=0.042, N=6, Figure 2). For food sharing, no such link was found neither for female breeders (Rho=0.31, p=0.544, N=6) and males (Rho=0.77, p=0.072, N=6) nor for all breeders combined (Rho=0.45, p=0.140, N=12).

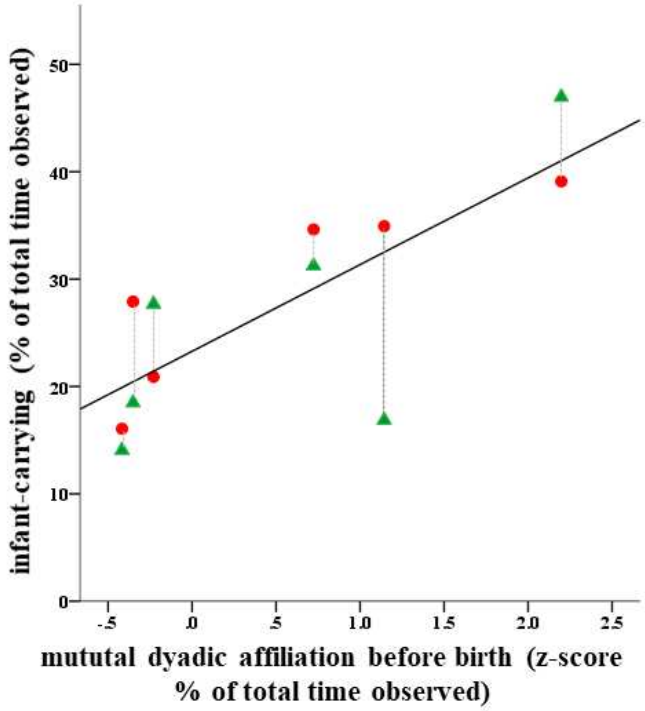

Figure 2: Positive link between mutual dyadic affiliation and infant-carrying in breeders. Pre-birth affiliation (z-score % of total time observed) among marmoset breeders is positively linked to infant-carrying (% of total time observed) in both females (red circles) and males (green triangles). Dotted lines connect breeding pairs.

Breeder-helper dyads

Investigating the link between breeder-helper relationship quality and breeder and helper cooperativeness, we found a positive effect only in male helpers. Specifically, male helpers shared more food after birth when they shared higher pre-birth levels of mutual dyadic affiliation with their female breeders (Rho=0.81, p=0.015, N=8, Figure 3), but not with their male breeders (Rho=-0.04, p=0.933, N=8). In contrast, their infant-carrying levels were not associated with pre-birth affiliation with female breeders or male breeders. No evidence was found for a positive link between pre-birth mutual affiliation and care-taking behaviors in dyads of female helpers and breeders.

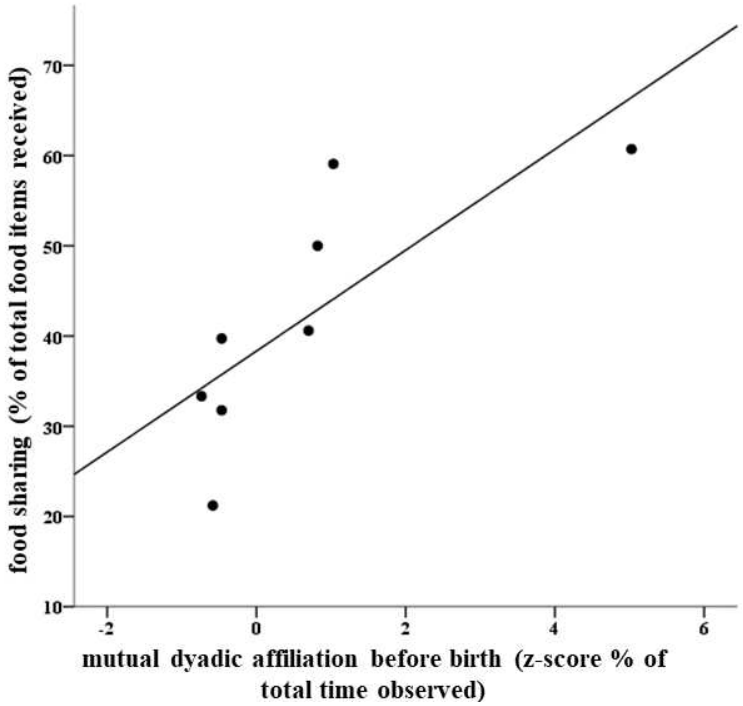

Figure 3: Positive link between mutual dyadic affiliation and food sharing in male helpers. Pre-birth mutual dyadic affiliation (z-score sec of total time observed) between female breeders and male helpers is positively linked to food sharing of male helpers.

4. Discussion

This study investigated how directed grooming and mutual dyadic affiliation between adult group members is associated with contribution to infant-care in cooperatively breeding common marmosets. In particular, we tested two strategic and two non-strategic hypotheses: the pay-for-help hypothesis, the pay-for-infant-access hypothesis, the intrinsic predisposition hypothesis, and the relationship quality hypothesis. Our findings reveal a positive link between relationship quality and infant-care contribution in marmoset care-takers, whereas strategically directed grooming (as payment for help or for infant-access) and individual intrinsic prosocial predispositions showed no such effects.

429 According to the pay-for-help hypothesis, female breeders were expected to groom
430 male breeders more than vice versa, and males contribute more to infant-care the more
431 grooming they received. Likewise, it predicted that breeders of both sexes groom helpers
432 more as incentive to help. We found that male breeders who received more grooming from
433 their mates before birth engaged more in infant-carrying and food sharing. However, unlike as
434 predicted, a similar effect was also found in female breeders who likewise carried more if
435 they had received more grooming from male breeders prior to birth. This result is more
436 consistent with the relationship quality hypothesis than with the pay-for-help hypothesis.
437 Furthermore, male breeders, but not females, groomed helpers more in the pre-birth period,
438 but grooming from breeders to helpers was not positively associated with infant-care
439 contribution in helpers. Rather, we found a weak negative effect. Thus, receiving more
440 grooming from breeders did not predict contributions to care-giving or other cooperative
441 activities in helpers. Together, these results do not support the pay-for-help hypothesis.
442 According to the pay-for-infant-access hypothesis, we expected helpers, especially
443 females, to groom their parents more than vice versa before and after birth, and we expected
444 grooming given to parents to be positively linked to infant-carrying in helpers. We found no
445 evidence to support this hypothesis, since neither pre- nor post-birth grooming was more
446 directed from helpers to parents than vice versa. Furthermore, grooming from helpers to
447 parents in both periods was not associated with more infant-access (i.e. carrying) by helpers
448 after birth. The same was true when only looking at female helpers, who are most likely to
449 have restricted access to infants [50, 72].
450 One explanation for this apparent lack of strategic behavior may be that pursuing
451 individual benefits is too (cognitively) costly when the marginal gains are rather modest.
452 Hence, cooperative breeders may generally not be very strategic, especially in the presence of
453 dependent offspring, and their prosocial motivation may be facilitated by the degree of social
454 integration and bondedness with other cooperation partners.

According to the intrinsic predisposition hypothesis, stable individual differences in prosociality should be reflected both in grooming levels directed towards other group members and in infant-care contribution. Our results do not support this prediction, since individuals who on average groomed others more were not at the same time more likely to engage in infant-care. This is consistent with the recent finding that experimentally assessed dyadic prosociality in marmosets is dyad- rather than individual-specific [34]. Together, this indicates that an individual's readiness to contribute to infant-care is not a stable individual trait but more flexible and mainly regulated by factors such as sex and status [7], group composition [73], and dyadic interactions with specific group members, as investigated in the relationship quality hypothesis.

According to the relationship quality hypothesis, pre-birth mutual dyadic affiliation (as indicator of relationship quality) is expected to be positively linked to individual care-taking contribution in both partners, both in breeding pairs and breeder-helper dyads. Positive evidence for this hypothesis was found in breeders, where both females and males carried infants more and shared more food after birth when they were engaged in highly affiliative relationships with their mates. Similar effects were found in dyads including parents and male helpers: male helpers shared more food after birth when they were engaged in more affiliative relationships with their female breeders. These findings suggest that relationship quality rather than strategically directed grooming is related to cooperativeness in marmoset care-takers. This is also consistent with the finding from Ginther and Snowdon [41], who reported a positive link between maternal grooming and carrying contribution of male helpers in the previous litter. In contrast, two studies showed that tamarin male breeders even groomed male helpers more if they were previously less engaged in care-taking, possibly to prepare unexperienced male helpers for their social role as care-takers [41, 74]. The authors suggest that, on the proximate level, greater comfort and physical contact among care-takers may be

480 more rewarding than specifically directed grooming, which is consistent with the relationship
481 quality hypothesis.

482 Interestingly, the positive correlation with relationship quality was specifically found
483 for breeding pairs and adult male helpers - the most important helpers in marmoset groups [1,
484 75, 76]. Our recent findings suggest that group-living marmosets form differentiated dyadic
485 relationships [31] that are also stable up to six months [34], not only between breeders but
486 also in other dyad types. Hence, the maintenance of high quality relationships may be an
487 important basis for successful cooperation during infant-care, in breeders as well as other
488 main care-takers in marmoset groups.

489 The positive link between relationship quality and infant-carrying in breeding pairs
490 was consistently reflected in pre-birth dyadic affiliation but also in pre-birth directed
491 grooming levels that were linked to helping in the dyad partners or grooming recipients,
492 respectively. These findings indicate that female breeders do not simply use grooming as
493 incentive for male breeders to help, but that both parents may "reassure" their bond mutually
494 prior to birth. Furthermore, the findings suggest that parents who are stronger bonded to each
495 other are also more committed to parenting after birth. Consistent with the relationship quality
496 hypothesis, this effect was equally present in females and males. The finding that food sharing
497 was only related to relationship quality in male helpers may indicate that a cooperative and
498 cohesive group climate particularly facilitates proactive food provisioning in marmoset males.
499 In female breeders, the relationship hypothesis may be less evident because of stronger
500 energetic constraints, which are also reflected in their lower levels of food sharing [6, 71].

501 Relationship quality between breeders and female helpers was not associated with
502 food sharing in female helpers like it was in male helpers. In fact, our data even indicate that
503 female helpers who received *more* grooming from their fathers before birth contributed *less* to
504 food sharing. Overall, female and male marmoset helpers show equally high levels of food
505 sharing when infants are present, whereas female helpers contribute considerably less to

506 infant-carrying, even though they are presumably highly motivated [6]. Temporarily high
507 food sharing levels in female helpers may thus be caused by additional individual interests,
508 such as gaining access to young infants [6]. This might be particularly important for less well
509 integrated female helpers, who receive less grooming from male breeders, and could explain
510 the lack of a link between grooming from male breeders and food sharing in female helpers.
511 Hence, strategic and non-strategic effects, as we postulate them in our four hypotheses, are
512 probably not mutually exclusive, and further studies are required to better understand sex-
513 specific differences of the role of relationship quality and additional individual interests in
514 marmoset helpers.

515 Beside the social factors discussed above, affiliative interactions and cooperation also
516 underlie substantial physiological regulation. For example, strategic and risk taking behavior
517 is related to higher testosterone levels, e.g. as shown in men [77], and to higher nutritional
518 status, e.g. as shown in chimpanzees [78]. The hormone prolactin is known to be positively
519 associated with infant-care in marmoset fathers and helpers [79-84], presumingly by fostering
520 non-strategic behavior. Particularly interesting in this context is also the neurohormone
521 oxytocin (OT), which is generally positively involved in the regulation of affiliative and
522 cooperative behaviors and of stress coping in primates [85-89] and other mammals [90-92],
523 including humans [93-95]. Our recent findings show that elevated oxytocin levels of adult
524 marmoset care-takers are associated with proactive food sharing with infants [6], and that
525 strongly bonded marmosets have synchronized oxytocin levels over time [31]. These findings
526 and two studies from chimpanzees [86, 89] emphasize the influence of partner-specific
527 bonding on OT effects related to cooperative interactions, which directly supports the
528 relationship quality hypothesis. OT may thereby also act on the intrinsic motivational level, as
529 we discussed elsewhere [6]. Moreover, the multiple regulatory functions of OT in positive
530 social interactions may lead to potential “spillover” or cross effects, i.e. high-quality
531 relationships and intense affiliative interactions among bonded partners may indirectly

facilitate prosocial and cooperative behavior in the individuals involved [96]. Further research will be necessary to investigate these questions and the role of physiological regulators in strategic and non-strategic affiliative interactions in more detail.

5. Conclusion

Overall, we conclude that individual differences in care-taking contribution among marmoset group members cannot be explained by strategic behavior as predicted by the pay-for-help or the pay-for-infant-access hypothesis, nor are individual differences in intrinsic prosocial predispositions sufficient to explain this variation. Rather, our findings support the relationship quality hypothesis and suggest that individual prosociality and cooperation are related to relationship quality among specific cooperation partners. Further studies will be important to explore the effects of social bonds on prosociality and cooperation in callitrichids in more detail, and to investigate their implications on other cooperative breeding species, such as humans.

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